

Two abnormal Plutei of Echinus, and the light which they throw on the Factors in the normal development of Echinus.

By

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With Plate 24 and 2 Text-figures.

THE present paper deals with two remarkable larvæ, the first a larva of *Echinus miliaris* obtained in a culture reared from eggs fertilised in the Zoological Laboratory of the Imperial College of Science and Technology, and the second a larva of *Echinus esculentus* obtained in a culture of eggs fertilised in the Laboratory of the Marine Biological Station at Plymouth. The second and more interesting specimen I owe to the kindness of Mr. de Morgan, by whom the culture in which it appeared was instituted.

I shall first deal with the larva of *Echinus miliaris*. The sea-urchin from which the eggs were obtained was sent alive from Plymouth to London. Here the eggs were fertilised with sperm from another individual, which also came from Plymouth, and the resulting larvæ were transferred to half-gallon jars of green bottle-glass containing sterilised sea-water to which a culture of the diatom *Nitzschia* had been added. The jars were placed in a sink into which water was constantly dropping from a tap and they were covered in. Here the larvæ developed for some weeks until a six-armed

pluteus was formed, and then a certain number were transferred to an eight-gallon jar fitted with a plunger containing similar sterilised sea-water to which a mixture of *Nitschia* and *Pleurococcus* cultures was added. This jar was also covered in, and the cover as well as three fourths of the periphery were sheathed in black paper in order to protect the larvæ from the baneful effects of too much light. In this jar the abnormal larva first to be described was found, and in the same jar a week or two later thirty or forty fully metamorphosed echini were found creeping about. To the best of my knowledge this is the first time that the eggs of a sea-urchin have been reared through the whole of their development until the completion of the metamorphosis in an inland laboratory.¹ It is to be noted that whilst the sea-urchins came from Plymouth, on the English Channel, the sea-water came from Lowestoft, on the North Sea. The water was purified by shaking it with animal charcoal, which was allowed to settle; then the supernatant liquid was decanted off and passed under pressure through a Berkfeld filter. In this way the water was cleansed from all bacteria, and also from all soluble organic toxins, and when in this purified condition it received the culture of diatoms which is to serve as food for the larvæ.

It will be noted that the method employed for rearing the larvæ is a combination of the one used by me in Plymouth in 1898 and 1899 (5), and the one recommended by Dr. Allen (1); I take this opportunity of expressing my indebtedness to Dr. Allen for his assistance and advice in the matter of fitting up the salt-water aquaria in the Imperial College.

Dr. Allen keeps the larvæ in the half-gallon jars until they

¹ Since writing this sentence I have learned, through a letter of Prof. Stanley Gardiner to 'Nature' (July 27th, 1911), that a single hybrid between the species *Echinus miliaris* and *Echinus esculentus* had been reared through its entire development in the Zoological Laboratory of the University of Cambridge a week or two before my specimens had completed their development.

have completed their development. I find that in these jars they develop very well until the so-called "echinus-rudiment" has attained a large size, and then degeneration in many cases sets in. The ectoderm of the larval arms becomes retracted and gradually devoured by phagocytes, then the "echinus-rudiment" itself is attacked; the larva sinks to the bottom and drags out an invalid existence for a week or two as a helpless cripple, consisting of merely the trunk and the larval alimentary canal. The cause of degeneration is somehow connected with the too luxuriant growth of the diatom in a confined space.

On the other hand, the method which I employed in 1899 is very laborious, inasmuch as it requires constant removal of the bottom layer of the water in the culture jar, and its replacement by clean sea-water taken from a long distance off from the shore, and it is impossible to apply in an inland station. If, however, the larvæ are brought on in the half-gallon jars till all the larval arms are fully formed, and then transferred to the eight-gallon jar with the plunger, in which a culture of diatoms has been placed some time previously, then the happiest results are obtained. It is to be noted that if insufficient food be present in the large jar, the larval arms become fully developed and very long, but the "echinus-rudiment" remains in an infantile condition, showing that the pathological absorption of the larval arms which occurs so frequently in the half-gallon jars is not due to want of food, but to toxic conditions connected with want of space.

The abnormal larva shown in fig. 1 is normal in every respect save that of the echinus-rudiment. The eight arms pertaining to the fully-developed *Echinopluteus* larva are all present and long and equally developed. The larva is represented as seen from the dorsal surface, and one can see the long antero-lateral arms (*a.l.*), and behind them the præoral arms bending forward above the mouth (*pr.o.*). At the sides of the larva are seen the postero-dorsal arms (*p.d.*), whilst behind all tower up the anal or post-oral arms (*p.o.*). The whole course of the ciliated band can be seen. Below it

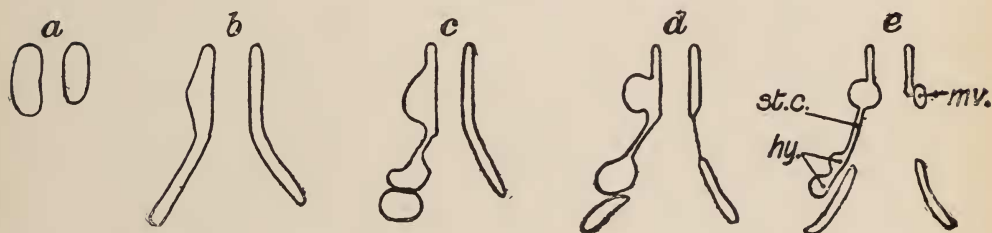
on each side of the larva are the two ciliated epaulettes, which at one time formed part of the band, but which have become completely separated from it, and serve as main locomotor organs for the larva in this stage of its development. One on each side, the dorsal, is situated in front of the postero-dorsal arm, and one, the ventral, is behind the post-oral arm. Between them the ciliated band dips down in a deep loop. Within the curve of this loop is the "echinus-rudiment" on the left side, consisting of the hydrocœle, which appears as a flattened, thick-walled vesicle, with an almost virtual lumen and an ectodermic invagination—the amniotic cavity, the inner end of which is pressed against the hydrocœle. The abnormality of the larva consists in the fact that a precisely similar "echinus-rudiment" is situated on the right side, where in the normal larva at this stage one would expect to find nothing of the sort. Through the transparent dorsal integument the larval œsophagus and stomach can be seen. Both are perfectly normal. At the sides of the œsophagus can be seen the thickenings which carry the two halves of the adoral band of cilia (*ad.*, fig. 1).

External to this thickened band on each side can be seen the outline of the anterior cœlom (*l.a.c.*, *r.a.c.*). Near the middle line above the stomach can be seen a small circular pore (*m.p.*). This is the primary madreporic pore.

Now when treating of the normal development of Echinus I have shown (5) that after the cœlom has been separated from the archenteron it divides into right and left sacs, and that the left sac acquires a communication with the exterior by the formation of a vertical canal, the pore-canal, which fuses with an ectodermic invagination. Subsequently each sac divides into anterior and posterior portions and the pore-canal communicates with the hinder part of the anterior portion of the cœlom on the left side. The anterior cœlomic sacs apply themselves to the larval œsophagus, to which they supply muscles, whilst the posterior sacs come to lie at the sides of the stomach. From the hindermost portion of the left anterior sac a vesicle is partially constricted off; this is

the hydrocœle or rudiment of the water-vascular system of the adult. The persistent neck uniting it with the rest of the left anterior cœlom becomes the stone-canal. From the hinder end of the right anterior cœlom a solid cellular outgrowth is formed, which becomes hollowed out into a vesicle and comes to lie at the right of the madreporic pore. This is the so-called "dorsal sac" or "madreporic vesicle," which I regard as a rudimentary antimeric of the hydrocœle on the right side. I have shown that in *Asterina gibbosa* (4) and in *Ophiothrix fragilis* (6) it may occasionally take on the form of a hoop with five lobes, thus copying

TEXT-FIG. 1.



Five diagrams showing the changes undergone by the cœlomic sacs of the Echinopluteus larva. *st. c.* Stone-canal. *hy.* Left hydrocœle. *mv.* Madreporic vesicle or right hydrocœle.

the embryonic form assumed in these genera by the left permanent hydrocœle. The changes undergone by the cœlom in the normal larva of *Echinus* are shown in Text-fig. 1, reproduced from my paper on the subject referred to above (5).

Now, in the living larva and in whole mounts of larvæ, preserved in strong formalin, it is perfectly easy to see this madreporic vesicle lying at the side of the madreporic pore; but in the abnormal larva which we are considering no trace of such a structure was to be seen. We conclude, therefore, that in this individual the madreporic vesicle has taken on the same form as the normal left hydrocœle, and is therefore represented by the hydrocœle to be seen on the right side

of the stomach in fig. 1. For such a larva the term "enan-tiomorphous" has been suggested. I have described enantiomorphous larvæ of *Asterina gibbosa* and of *Ophiothrix fragilis*, but this is the first time that such a larva has been recorded in the case of a species of Echinoid. This larva, then, affords a proof—if proof were needed—that the view which I put forward as to the homology of the madreporic vesicle or dorsal sac is correct. If, then, the larva in the three groups of the Asteroidea, Ophiuroidea and Echinoidea carries a vestigial right antimer of the hydrocœle, it is a fair conclusion that in the free-swimming ancestor of the Echinodermata the hydrocœle was a paired structure. But the double hydrocœle, equally developed on each side, was lost as soon as the free-swimming habit was given up and the fixed stage had been attained, for it was almost certainly due to the atrophy of the right hydrocœle that the left hydrocœle, from being a hoop, became a ring. Now we have no reason whatever to believe that the primitive bilateral ancestor of Echinodermata possessed an amniotic cavity; this is a peculiarity of Echinoidea, for in both Asteroidea and Ophiuroidea the skin covering the hydrocœle is flush with the general surface of the body, and this is obviously a more primitive condition than to have an amnion. The interest, therefore, in our abnormal larva deepens, for though the double hydrocœle is an ancestral atavistic feature, the double amniotic cavity cannot possibly be. Now if we had not such larvæ as the one which we are considering to guide us and if we were endeavouring to unravel the factors in normal development, we should note the fact that the hydrocœle is formed before a trace of the amniotic cavity is visible. We should therefore conclude either that the amnion is due to an influence on the ectoderm emanating from the hydrocœle, or that there is a spot in the ectoderm predestined to form the amnion, though we cannot distinguish it from other spots with the naked eye. Our larva, however, leads us to decide in favour of the first of these two alternatives, and we are thus led to the conclusion that the formation of the ectodermic

cavity, known as the amnion, is the result of a stimulus acting on the ectoderm and emanating from the hydrocœle, and that the whole ectoderm of the larva is so organised that any part of it can form an amniotic cavity if the appropriate stimulus reaches it. Only in this way can we account for the formation of an amniotic cavity on the right side. The larva was cut into transverse sections, after being drawn, as shown in fig. 1; unfortunately the method of preservation (strong formalin followed by strong alcohol) yielded such unsatisfactory results that nothing was learnt beyond what could be made out from the whole amount. I have come to the regretful conclusion that for delicate larvæ like *Echinoplutei* no other reagent is available save osmic acid followed by Müller's fluid, which occasions brittleness, but gives thoroughly satisfactory results as regards histology.

We now turn to the second larva described in this paper. This is a larva of *Echinus esculentus*, fifty-five days old, which was preserved in alcohol. After making the two drawings of it, represented in figs. 3 and 4, I was attempting to detach it from the slide for the purpose of having it cut into sections when it was accidentally lost. While regretting the accident, I consider it quite certain, from my experience with the other larva, that the preservation was too poor for any additional information to have been gleaned from sections. Fig. 2 represents a posterior view of this larva when it was thirty-five days old. This drawing was made from the living specimen by Mr. de Morgan, and my best thanks are due to him for his permission to use this sketch in illustrating my paper. The larva is normal in every way except for the presence of two "echinus rudiments," seen as dark lobed masses, one situated at each side of the alimentary canal. The alimentary canal is also dark-coloured, owing to the fact that it is crammed with *Nitschia*. The "echinus-rudiment" lying on the left side of the larva (*ech.*), that is, on the right side of the figure, is larger than the other abnormal one (*ech.*,¹) which is situated on the right side of the larva, and consequently on the left side of the

figure. The præoral (*pr.o.*), antero-lateral (*a.l.*), postero-dorsal (*p.d.*), and post-oral arms (*p.o.*) are seen to be perfectly normal, except that, as frequently happens with larvæ that are reared throughout their whole larval existence in half-gallon jars, they are somewhat shorter than usual. The two ventral ciliated epaulettes have met in the mid-ventral line above the anus, and behind and partly obscured by them are seen the dorsal epaulettes. Above the united ventral epaulettes can be seen the mid-ventral portion of the ciliated band, whilst below them can be seen the right and left posterior ciliated epaulettes, which are characteristic of the larva of *Echinus esculentus*, and serve to distinguish it from the larva of *Echinus miliaris*, whilst at the posterior pole of the larva can be seen one of the three pedicellariæ (*ped.*), which appear before the larval phase has been passed through. The other two are situated on the right side of the larva, and one of these (*ped.*¹) can also be seen. Although partly obscured by the mid-ventral portion of the ciliated band, the larval mouth (*st.*) can be seen. It is obvious that the larva before us represents what the larva of *Echinus miliaris*, which has been just described, would have grown to had it been permitted to live. The difference between the two (apart from the specific differences between the larvæ of *Echinus miliaris* and *Echinus esculentus*) consists merely in the greater growth of the "echinus-rudiments" in the case of the second larva. When this larva came into my hands it had attained the age of fifty-five days; the larval arms were being absorbed, and the roofs of the amniotic cavities had also been absorbed, so that the tube-feet on either side were exposed; in a word, the larva had attained the stage where, if it had been a normal larva, it would have metamorphosed into a young sea-urchin.

Fig. 3 represents a view of the larva in this stage seen from the left side. The oral lobe, carrying the præoral and antero-lateral arms, is seen above, and beneath the præoral arms the larval mouth and the œsophagus with the adoral ciliated bands can be seen. Below the oral lobe the body of

the larva takes on a discoid form; this disc is the oral disc of the young Echinus formed out of the floor of the amniotic cavity. The ciliated band of the larva is seen to make a wide sweep round it, which is merely the enlarged re-entrant loop, which, in an undeveloped state, was noted in the larva of *Echinus miliaris*. On this loop can be seen the reduced stumps of the postero-dorsal post-oral arms. Outside it can be seen the dorsal (*d.ep.*), and ventral (*v.ep.*), and posterior ciliated epaulettes (*p.ep.*). The ventral ciliated epaulette is bent on itself in the shape of a U; this is almost certainly a result of the contraction caused by the preservative (spirit) used. Turning our attention now to the disc of the "Echinus-rudiment," we notice the five primary unpaired tube-feet (*pod.*). Each is flanked by a pair of smaller tube-feet (*pod.*¹); these are the first paired tube-feet and eventually become the oral or gustatory tube-feet of the adult, whereas the primary tube-foot is destined to degenerate into the insignificant knob in which the radial canal terminates. In the centre of the disc of each primary tube-foot is a pointed sense-organ, consisting of elongated ectoderm cells. In the intervals or inter-radii which intervene between adjacent primary tube-feet there are groups of spines—four in each inter-radius constructed on the same model as the spines of the adult; in fact they are the first adult spines. Each consists of a shaft supported by a fenestrated calcareous rod, attached to a boss by a thick collar consisting of radiating muscles. All the calcareous matter had been dissolved away when the larva reached me, but the calcigenous cells (*calc.*) can be seen through the transparent ectoderm. It will be noticed that the four spines are arranged in the form of a lozenge ∙ ∙ in each inter-radius. Within the circle formed by the tube-feet and the spines a circular band is to be seen; this is the nerve-ring of the adult shining through (*nerv.*). Within this again a pentagonal figure, subdivided into five secondary pentagons, is situated. These I interpret as the five dental pockets which together constitute Aristotle's lantern, and within these the adult

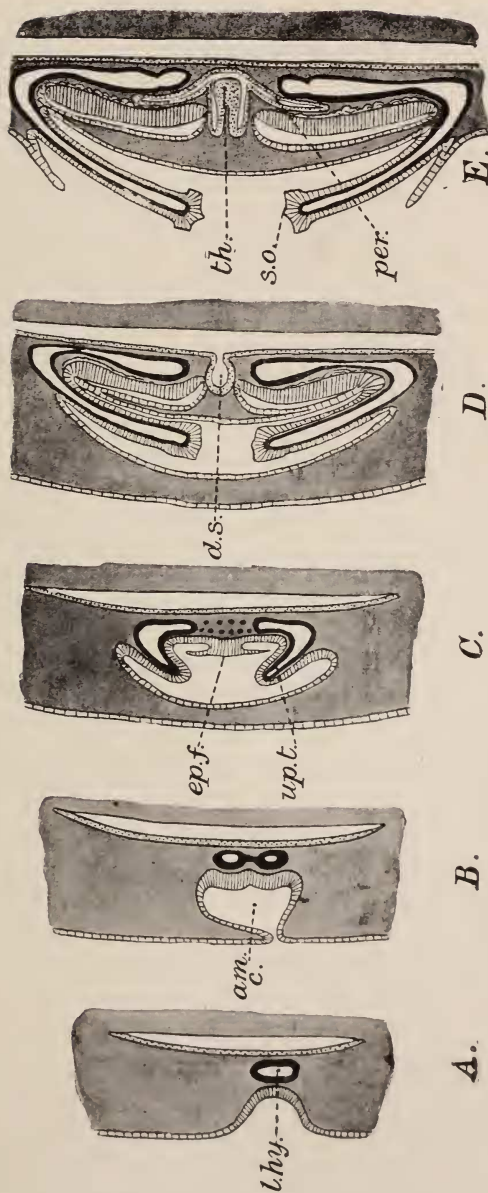
œsophagus and mouth (*m.*) can be made out. All the structures which I have just described can be seen in a normal larva of this age when viewed from the left side, but the peculiarity of the larva under discussion is this: that when, as is represented in fig. 4, it is viewed from the right side, an almost precisely similar set of structures can be seen. It is, of course, not quite easy to get the larva to lie flat on either side, and as a matter of fact in fig. 3 it is tilted so that the ventral surface of the oral lobe is half turned towards the observer, and we see into the larval mouth (*st.*), whereas in fig. 4 the dorsal surface of the oral lobe is presented to our view, and the larval œsophagus is seen glimmering through it. The same arrangement of spines and tube-feet can be seen on the right side as on the left, and within them a circle representing a second nerve-ring; within this a pentagon representing a second but rather smaller Aristotle's lantern; and finally within this a second adult œsophagus and mouth. The only differences between the left and the right discs which I could detect was the smaller radius of the nerve-ring, and the smaller size of the contained Aristotle's lantern on the right side.

Now we have already concluded from the study of the abnormal larva of *Echinus miliaris* that whereas the appearance of a second hydrocœle is probably a reminiscence of a state of affairs which obtained in the free-swimming ancestor of all Echinoderms, the appearance of a second amniotic cavity could not be interpreted in that sense. It is still clearer that the appearance of the peculiar spines of the adult Echinoid on the right side cannot be an atavistic feature, and still less the appearance of a second Aristotle's lantern and second "adult œsophagus."

In order to show what relationship to each other the various structures sustain which together make up the complex known as the "echinus-rudiment," I reproduce here a text-figure from my paper (5) on the development of *Echinus esculentus*.

From these diagrams we see that the amniotic cavity

TEXT-FIG. 2.



Five diagrams showing the growth and differentiation of the "echinus-rudiment." *am.c.* Amniotic cavity. *d.s.* Dental sac. *ep.f.* Epineural fold. *l.hy.* Left hydrocoele. *per.* Perihamal canal. *s.o.* Sense organ on tube-foot. *th.* Tooth. *up.t.* Unpaired tube-foot.

deepens and becomes completely closed off from the exterior; the hydrocœle becomes five-lobed (only two of these lobes are represented as cut by the sections), the free ends of these lobes grow and protrude into the amniotic cavity, and in this way the unpaired tube-feet are formed. Between two adjacent tube-feet an ectodermic fold is developed from the floor of the amniotic cavity; this is the epineural fold. Its crest sends out two flaps which meet those of the other epineural folds, and thus the original floor of the amniotic cavity is completely covered in by a new fold which forms a new floor at a higher level, and eventually forms the free surface of the ventral part of the young sea-urchin.

The wall of the left posterior cœlom of the larva, which impinges on the inner side of the hydrocœle, now begins to undergo changes. Opposite the base of each epineural fold, an evagination of the cœlom is formed. This is the rudiment of one of the five tooth-pockets or dental sacs, which together form Aristotle's lantern. The evagination is cut off from the rest of the cœlom. Then its external wall becomes thickened and projects into its cavity. This projection is the rudiment of the tooth. From the sides of the tooth-socket canals are given off which insinuate themselves between the lobe of the hydrocœle and the original floor of the amniotic cavity, now roofed over by the epineural false floor. These canals are the radial perihæmal canals, and the portion of the original floor of the amniotic cavity lying above them becomes converted into the radial nerve-cord of the adult. It will thus be seen that the growth of the "Echinus-rudiment" is an extremely complex process, involving not only the hydrocœle and the ectoderm above it, but also the external wall of the left posterior cœlom, and finally, when the adult œsophagus is formed, the external wall of the larval stomach also. The calcigenous tissue which fills the interior of the spines which are placed in the intervals or inter-radii between the unpaired tube-feet is mesenchyme budded from the wall of the left posterior cœlom, whilst the external covering of the spines is, of course, ectoderm from the

floor of the amniotic cavity. Now, when we consider that an "echinus-rudiment" has been formed on the right side of our larva, almost precisely similar to that which is normally formed on the left side, and which is typically developed in our larva, we are driven to the conclusion that not only is the ectoderm on the right side of the larva capable of forming an amniotic invagination—a conclusion which we had already reached from the consideration of the other larva—but that the right posterior cœlom is capable equally with the left of budding off calcigenous mesenchyme, and of giving rise to evaginations which form dental pockets, and that the right side of the stomach equally with the left is capable of giving rise to a protrusion forming an adult œsophagus.

Under ordinary circumstances none of the tissues of the right side of the larva undergo this development, and the reason that they do so in this case must be due to some kind of influence emanating from the abnormally developed right hydrocœle. If, then, the appearance of a right hydrocœlic vesicle can so totally change the development of tissues which normally would have had quite a different fate, it is reasonable to conclude that the development of organs on the left side of the larva is due to a similar influence radiating from the left hydrocœle. The final conclusion to which we are led is, therefore, that the larva consists of sheets of uniform tissues, and that particular areas of these sheets are acted on by localised stimuli so as to be transformed into adult organs; or putting the conclusion in another way, the particular course that development takes in an Echinoderm larva, is only one out of many possibilities, and by no means exhausts the potencies of the embryonic layers, and there is a certain rude analogy between the maintenance of a race by the preservation of a few individuals out of many born, and the development of an individual through the realisation of a few of the many potencies of the embryo. As mentioned above, I have found enantiomorphous larvæ in the case of *Asterina gibbosa*. In one of these, development has proceeded so far that not only do the lobes

of both hydrocœles project freely as tube-feet, but on the right side as well as on the left evaginations of the external cœlomic wall are formed, which give rise to perihæmal pockets. Therefore here, too, under the stimulus of an abnormally developed right hydrocœle, the right posterior cœlom has acquired powers of which, under ordinary circumstances it appears to be totally destitute. Now the perihæmal pockets of an Asteroid are homologous with the dental pockets of an Echinoid, but in an Asteroid these pockets never form teeth in their interior, but give rise to the so-called external perihæmal ring. If we regard Echinoids as developed from Asteroids, as in my paper on *Echinus esculentus* (5) I have given reason for doing, then the evolution of an Echinoid from an Asteroid must have consisted to a large extent of an alteration in the chemical constitution of the embryonic tissues, so that these have come to react differently to the stimulus exerted on them by the hydrocœle. No doubt the hydrocœle itself has been also altered, so that the stimulus emanating from it is different in the two cases.

Now a general review of the structure of the simplest and oldest stalked Echinodermata known has led Bather (2) to the view that the body of an Echinoderm was not at first dominated by radial symmetry, but only became so secondarily when the appendages of the hydrocœle had attained a radially symmetrical arrangement. The early palæontological history of free Echinoderms (Eleutherozoa) is still unknown, but there is no reason to believe that it differed in this respect from that of fixed Echinoderms (Pelmatozoa). We thus arrive at the interesting conclusion that the influence of the hydrocœle on the other tissues, which, in the development of the race, has led to the formation of the beautifully symmetrical Crinoid out of the somewhat shapeless sac-like primitive Pelmatozoon, plays an equally important part in the fashioning of the individual out of the undifferentiated embryonic tissues. Driesch (3), as is well known, attributes the regulation of individual development to an indwelling "entelechy," a rudimentary "knowing and willing," which, out of the materials presented

to it, builds up an individual. We can only remark that if this be the case our second larva is an instance where the entelechy has been deceived, and has been led to construct a creature which could not possibly have survived.

MILLPORT, SCOTLAND,

July 17th, 1911.

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EXPLANATION OF PLATE 24,

Illustrating Prof. E. W. MacBride’s paper on “Two Abnormal Plutei of Echinus.”

KEY-LIST OF ABBREVIATIONS USED IN ILLUSTRATION OF THE FIGURES.

Ad. Adoral band of cilia. *a.l.* Antero-lateral ciliated arm. *am.* Amniotic cavity. *am.*¹ Amniotic cavity abnormally developed on the right side of the larva. *calc.* Calcigenous cells in the interior of the adult spines. *d.ep.* Dorsal ciliated epaulette. *ech.* “Echinus-rudiment” on the left side of the larva. *ech.*¹ “Echinus-rudiment” abnormally developed on the right side of the larva. *l.a.c.* Left anterior celom of the larva. *l.hy.* Left hydrocele. *m.* Adult mouth. *m.p.* Madreporic pore. *nerv.* Adult nerve-ring. *p.d.* Postero-dorsal ciliated arm. *ped.* Median dorsal pedicellaria. *ped.*¹ Lateral pedi-

cellaria. *p.ep.* Posterior ciliated epaulette. *p.o.* Post-oral ciliated arm. *pod.* Unpaired tube-foot. *pod.*¹ Paired tube-feet. *pr.o.* Præoral ciliated arm. *r.a.c.* Right anterior cœlom. *r.hy.* Right hydrocele. *sp.* Adult spines. *st.* Stomodæum, i. e. larval mouth. *v.ep.* Ventral ciliated epaulette.

Fig. 1.—An abnormal pluteus of *Echinus miliaris* viewed from the dorsal surface and magnified 110 diameters. *Am., am.*¹ Left and right amniotic cavities. *m.p.* Madreporic pore.

Fig. 2.—An abnormal pluteus of *Echinus esculentus* viewed from the ventral surface. Drawn from life by Mr. de Morgan and magnified 110 diameters. *Ech., ech.*¹ The two "echinus-rudiments." *p.ep.* The posterior ciliated epaulette characteristic of *Echinus esculentus*, *st.* Larval mouth.

Fig. 3.—The same pluteus as that represented in fig. 2 at a later stage of development, viewed from the left side and magnified 110 diameters. *m.* Adult mouth in the centre of Aristotle's lantern. *nerv.* Nerve-ring. *p.d.* and *p.o.* Disappearing remnants of postero-dorsal and post-oral ciliated arms. *sp.* Adult spines.

Fig. 4.—The same pluteus as that represented in fig. 3 at the same stage of development viewed from the right side; magnification 110 diameters. *Ad.* Adoral ciliated band shimmering through. *m.* Second adult mouth. *nerv.* Second adult nerve-ring. *pod.* Unpaired tube-foot *pod.*¹ Paired tube-feet.